UNIVERSITÉ DU QUÉBEC À MONTRÉAL

COMPARAISON DES EFFETS D'UNE ÉPIDÉMIE DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE (*Choristoneura fumiferana* (Clem.)) À CEUX DE LA COUPE AVEC PROTECTION DE LA RÉGÉNÉRATION ET DES SOLS

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

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JONATAN BELLE-ISLE

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RÉSUMÉ

Les perturbations naturelles sont aujourd'hui reconnues comme étant des parties intégrantes de la dynamique des forêts, voire même essentielles à la diversité et au fonctionnement des écosystèmes. C'est pourquoi depuis quelques années, on croit que la meilleure façon de conserver la biodiversité et les fonctions essentielles des écosystèmes forestiers soumis aux pratiques d'aménagement serait d'émuler les processus de perturbation naturelle se déroulant dans les forêts non aménagées. Bien que l'importance des perturbations intermédiaires soit de plus en plus reconnue, la plupart des travaux sur l'émulation des perturbations naturelles s'est concentrée sur le feu. Toutefois, un aménagement basé sur la compréhension des régimes des perturbations naturelles ne peut pas être axé exclusivement sur la dynamique des feux, ignorant le rôle des perturbations moins sévères ou survenant à de plus petites échelles.

Les épidémies de la tordeuse des bourgeons de l'épinette (TBE) constituent après les feux, la plus importante perturbation affectant la forêt boréale. Certains auteurs ont souligné des similitudes entre les épidémies sévères de la TBE et la coupe avec protection de la régénération et des sols (CPRS). Ces deux perturbations s'attaquent aux arbres matures en affectant peu ou pas la régénération préétablie et les sols. Pour arriver à modifier un aménagement forestier afin qu'il s'approche davantage d'un processus naturel, il est essentiel de caractériser précisément les différences et les similarités entre perturbations naturelle et anthropique. Nous proposons, dans le cadre de cette étude, de comparer les effets des CPRS à ceux des épidémies de la TBE dans les peuplements résineux de la sapinière à bouleau blanc dans la région de la Gaspésie. Puisqu'une éclaircie pré-commerciale (EPC) est systématiquement faite après chaque CPRS, et qu'il n'est pas possible de départager les effets de ces deux pratiques, la CPRS et l'EPC constituent ensemble la perturbation anthropique étudiée. Pour mieux comprendre les phénomènes écologiques impliqués dans ces deux types de perturbation, l'étude a été réalisée à deux échelles, soit celle du peuplement et celle du paysage. À l'échelle du peuplement, 10 stations issues de CPRS effectuées en 1989 et 10 stations sévèrement affectées par la plus récente épidémie de la TBE ont été étudiées. L'échantillonnage de données de végétation a permis d'évaluer les effets de ces perturbations sur l'abondance de matière organique telle que les chicots, les débris ligneux, les arbres résiduels, ainsi que la régénération retrouvée une quinzaine d'années après les perturbations. À l'échelle du paysage, l'interprétation de photographies aériennes a permis de caractériser la taille, la forme, et la distribution spatiale des ouvertures créées par ces perturbations. Les résultats obtenus montrent que les espèces compagnes du sapin baumier, soit l'épinette blanche et le bouleau à papier, ont été favorisées par l'épidémie de la TBE, tandis que les CPRS+EPC semblent plutôt favoriser la dominance du sapin. Les peuplements issus de l'épidémie présentent plus d'éléments structuraux tels que les arbres résiduels, les chicots et les débris ligneux en plus de présenter plus de variabilité horizontale sur le plan de la densité des tiges de plus de 2 m de haut. Les peuplements issus de CPRS+EPC présentent une plus grande diversité d'espèces d'arbre pour les strates inférieures alors que les peuplements issus de l'épidémie montrent une plus grande diversité pour les strates supérieures. Ainsi, nos résultats suggèrent que l'on devrait tenter de préserver les espèces compagnes lors de l'aménagement des forêts dominées par le sapin baumier, ainsi que certains éléments structuraux essentiels au fonctionnement des écosystèmes. De cette façon, il sera possible de

conserver la variabilité naturelle et la biodiversité végétale et animale de ces forêts, et ainsi favoriser la résilience de ces écosystèmes. À l'échelle du paysage, contrairement à ce que l'on s'attendait, les ouvertures créées par la TBE ont des formes plus régulières que celles créées par les CPRS. Par contre, étant donné leur taille grandement supérieure, les ouvertures créées par les CPRS ont tout de même moins de bordure par unité de surface. Ces résultats suggèrent que l'agrégation des unités de coupe devrait être limitée, comme dans le cas des coupes mosaïques. Par contre, les coupes mosaïques telles que pratiquées aujourd'hui, se font à une échelle trop grossière par rapport à la fine mosaïque créée par l'épidémie de la TBE.

SECTION I : INTRODUCTION GÉNÉRALE

La forêt boréale contient certains des derniers grands territoires peu peuplés de la planète dans lesquels les perturbations naturelles dominent encore aujourd'hui la dynamique des écosystèmes (Haeussler et Kneeshaw 2003). La prédominance des grandes perturbations naturelles telles le feu et les épidémies d'insectes, qui causent la destruction de grands étendues de forêt, laisse croire que ces écosystèmes pourraient supporter une exploitation forestière soutenue sans nécessairement dévier fortement de la dynamique des forêts naturelles (Pastor et *al.* 1998; Burton et *al.* 1999).

1.1 L'aménagement écosystémique

Les perturbations naturelles déterminent, entre autres, la taille, la forme, l'emplacement, et le type de parcelle qui constituent le paysage forestier, créant par le fait même de l'hétérogénéité dans le territoire (Lindenmayer and Franklin 2002). Les différentes composantes biologiques épargnées ou créées par les perturbations naturelles telles que les arbres résiduels, les chicots, les débris ligneux, et la régénération préétablie, créent dans les peuplements affectés une complexité structurale et des habitats pour de nombreux organismes vivants (Harman et *al.* 1986). La conservation de ces composantes biologiques essentielles est une problématique en regard des pratiques forestières traditionnelles (Lindenmayer et Franklin 1997). L'aménagement écosystémique cherchant à s'inspirer de la nature vise, entre autres, à maintenir les processus observés dans les différentes perturbations naturelles afin de conserver l'ensemble des éléments épargnés par ces événements, et ainsi conserver la complexité et l'hétérogénéité des peuplements et du paysage (Lindenmayer et Franklin 2002).

Pour guider l'émulation de perturbations naturelles dans les stratégies d'aménagement, il faut d'abord identifier les principaux types de perturbations caractérisant la dynamique des écosystèmes à aménager, et ensuite les comparer à l'aménagement que l'on désire modifier. Jusqu'à ce jour, la majorité des études caractérisant les différences et les similarités entre perturbation naturelle et anthropique comparent les effets des feux à ceux des coupes à blanc. Toutefois, certains auteurs mentionnent qu'on aurait peut-être accordé trop d'importance au rôle des feux dans la dynamique des forêts (Bergeron et *al.* 1998; Cumming et *al.* 2000; Haeussler et Kneeshaw 2003). Des recherches récentes démontrent que les perturbations naturelles intermédiaires sont plus fréquentes qu'on ne le croyait dans la forêt boréale, et dans certaines régions, plus importantes que le feu (Kuuluvainen 1994; Kneeshaw et Burton 1997; Kneeshaw et Bergeron 1998; Cumming et *al.* 2000; McCarthy 2001). Au Québec, des changements dans le régime des perturbations augmentent l'importance des perturbations intermédiaires dans le développement des peuplements forestiers (Kneeshaw et Bergeron 1996). Il semble que la fréquence des feux ait diminuée depuis l'Âge Glaciaire (Bergeron et Archambault 1993), tandis que la fréquence et la sévérité des épidémies de la tordeuse des bourgeons de l'épinette (TBE) auraient augmenté au cours du dernier siècle (Blais 1983; Morin et *al.* 1993). Les aménagements forestiers basés sur la compréhension des régimes des perturbations naturelles ne peuvent donc pas être axés exclusivement sur le régime des feux, ils doivent nécessairement tenir compte des perturbations secondaires telles les épidémies de la TBE.

1.2 Le domaine bioclimatique de la sapinière à bouleau blanc

La région à l'étude se trouve à l'intérieur du domaine bioclimatique de la sapinière à bouleau blanc qui se compose d'essences telles que le sapin baumier (*Abies balsamea* (L.) Mill.), le bouleau blanc (*Betula papyrifera* Marsh.), l'épinette blanche (*Picea glauca* (Moench) Voss) et l'épinette noire (*Picea mariana* (Mill.)). Le sapin baumier se régénère bien de façon naturelle (Ruel 1992). De plus, ses semis peuvent survivre plusieurs années sous couvert et ainsi permettre l'accumulation d'une abondante régénération préétablie (Hatcher 1960). Même dans des conditions d'éclairement réduit, le sapin baumier garde sa capacité à réagir à l'élimination du couvert, ce qui lui permet d'assurer la régénération du peuplement à la suite de perturbations comme la coupe, le chablis ou les épidémies d'insectes, lorsque celles-ci n'entraînent pas leur destruction (Gagnon 1985; Ruel 1992). Le bouleau blanc se régénère bien par rejets de souche (Perala et Alm 1990; Jobidon 1995), il peut donc constituer une part importante de la régénération après coupe (Laflèche et *al.* 2000). Par contre, l'émergence de nouveaux individus de bouleaux blanc est plus problématique puisque leur germination se fait principalement sur le bois en décomposition ou sur un sol minéral exposé par un chablis ou de la machinerie (Marquis 1965). La germination de l'épinette blanche est également facilité par l'exposition du sol minéral ou par la précense de bois décomposé (Eis 1967; Packee 1990 ; DeLong et *al.* 1997 ; Simard et *al.* 1998). Le simple passage de la machinerie lors de coupes avec protection de la régénération et des sols ou de coupes totales ne perturberait pas suffisamment le sol pour assurer un bon établissement des semis (Laflèche et *al.* 2000).

1.3 Les épidémies de la tordeuse des bourgeons de l'épinette (TBE)

La TBE (*Choristoneura fumiferana* (Clem.)) est un insecte indigène de l'est de l'Amérique du Nord causant la défoliation de ses arbres hôtes, soient le sapin baumier, l'épinette blanche, l'épinette noire et l'épinette rouge (*Picea rubens* Sarg.). La destruction répétée des pousses annuelles mène souvent à la mortalité des arbres hôtes puisqu'ils deviennent incapables de produire les ressources nécessaires pour assurer leur survie (Blais 1981; MacLean et Ostaff 1989). La TBE est généralement présente à de faibles niveaux de populations dans les forêts de sapin et d'épinette de l'est de l'Amérique du Nord (Morris 1963). Ainsi, le début d'une épidémie consiste généralement en l'augmentation graduelle des populations d'insectes (MacLean 1980). La mortalité des arbres hôtes survient aussi graduellement, et elle est généralement complétée dans les dix années suivant le début de l'infestation (MacLean 1980). Les forêts de sapin baumier sont bien adaptées aux épidémies récurrentes de la TBE et les peuplements matures affectés sont généralement régénérés après une épidémie (Morin et Laprise 1989). L'ouverture du couvert forestier due à la mortalité du sapin lors d'une épidémie permet à la régénération préétablie (généralement composée de sapins) de succéder à la canopée dévastée, et ainsi assurer une stabilité à long terme entre l'espèce hôte privilégiée et l'insecte (Baskerville 1975; MacLean 1980; Morin 1994). Selon Baskerville (1975), partout où la TBE peut atteindre un niveau épidémique, l'insecte détruit la forêt d'une façon qui assure le développement d'un nouveau peuplement des espèces hôtes pour les générations futures de l'insecte.

Mais la TBE ne fait pas qu'assurer le maintient de l'espèce hôte prévilégiée. D'après Holling (1973), la précense du sapin, qui est très compétitif, est favorisé entre les épidémies par rapport au bouleau et à l'épinette. Par contre, pendant les épidémies c'est le bouleau et l'épinette qui sont favorisés puisqu'ils sont moins ou pas susceptibles aux attaques de la TBE. Cette interaction entre ces peuplements forestiers et l'insecte aide à maintenir la présence de l'épinette et du bouleau qui, autrement, seraient probablement exclus par la compétition. Ce système semble très instable, puisqu'il fluctue beaucoup. C'est en fluctuant ainsi que les générations successives de forêt sont remplacées de façon à assurer une source de nourriture continue pour les générations futures de TBE. Ces fluctuations sont donc des caractéristiques essentielles qui maintiennent la persistance de la TBE, ainsi que de ses ennemies naturels, ses espèces hôtes, et les espèces d'arbres non hôte qui y sont associées.

1.4 L'aménagement forestier

Les coupes avec protection de la régénération et des sols (CPRS) semblent s'avérer efficaces pour reconstituer les sapinières à bouleau blanc puisque la structure de ses peuplements est relativement homogène et que la régénération préétablie y est souvent abondante (Hatcher 1960; Ruel et *al.* 1998). Une étude effectuée dans les sapinières de la Gaspésie au cours des années 1950 avait démontré que le renouvellement des sapinières boréales vierges après une coupe était assuré par la préservation d'une régénération résineuse préétablie (Webb 1961; MacArthur 1963). Laflèche et *al.* (2000) ont observé, cinq ans après une CPRS, une régénération de sapin baumier représentant une densité quatre fois supérieure à celle issue d'une coupe totale effectuée dans la même région (Archambault et *al.* 1998). D'autres coupes totales visant à protéger la régénération ont permis des taux de survie allant de 32 à 80% (MacDonnell et Groot 1997). Par contre, la régénération de sapin baumier bien établie avant la coupe offre une compétition de taille aux semis d'autres espèces comme l'épinette noire, rouge et blanche (McRae et *al.* 2001). Puisqu'actuellement, les sapinières tirent leur origine le plus souvent de CPRS, il est donc particulièrement intéressant de connaître la production des peuplements issus de cet aménagement (Doucet 1988). En Gaspésie, la CPRS est suivie d'une éclaicie pré-commerciale (EPC), pratiquée une dizaine d'année après la coupe, qui favorise le retour de peuplement dominé par les conifères.

1.5 L'émulation d'une perturbation naturelle

Les effets des CPRS+EPC s'approchent sensiblement de ceux d'une épidémie de la TBE (Baskerville 1975; MacLean 1984; Bergeron et *al.* 1999), puisque ces deux types de perturbations affectent principalement la canopée, et endommagent peu la régénération préétablie et les couches organiques du sol. L'objectif de cette étude est de caractériser précisément les différences et les similarités entre ces deux types de perturbations dans le but d'élaborer un aménagement forestier qui s'inspire d'un processus naturel constituant une partie intégrante de la dynamique des écosystèmes forestiers. Des perturbations de l'ampleur des épidémies de la TBE et des CPRS+EPC affectent les écosystèmes forestiers à plusieurs échelles. En fait, il n'y a pas d'échelle unique permettant d'observer et de comprendre les phénomènes écologiques (Levin 1992; Parker et Pickett 1998). Ainsi, la taille et la distribution des perturbations seront caractérisées à l'aide de cartes et de photos aériennes à l'échelle du paysage, tandis que l'abondance de matière organique résiduelle tels les chicots, les débris ligneux, les arbres vivants, et la régénération retrouvée à la suite de perturbations sera caractérisée à l'échelle du peuplement (Hunter 1993). Cette étude se fait en collaboration avec la compagnie forestière Temrex qui désire aller de l'avant et s'inspirer des résultats obtenus lors de ces travaux pour modifier leurs pratiques forestières.

Références

Archambault, L., Morissette, J. et Bernier-Cadoue, M., 1998. Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Québec, Canada. For. Ecol. Manage. 102: 61-74.

Baskerville, G.L. 1975. Spruce budworm-super silviculturist. For. Chron. 51: 4-6.

Bergeron, Y. et Archambault, S., 1993. Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the "Little Ice Age". Holocene 3(3): 255-259.

Bergeron, Y., Harvey, B., Leduc, A. et Gauthier, S. 1999. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. For. Chron. 75(1): 55-61.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. 11: 620-629.

Blais, J. R., 1983. Trends in the frequency, extend, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13: 539-547.

Burton, P.J., Kneeshaw, D.D. et Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. For. Chron. 75: 623-629.

Cumming, S.G., Schmiegelow, F.K.A. et Burton, P.J. 2000. Gap dynamics in boreal aspen stands : is the forest older than we think? Ecol. Appl. 10: 744-759.

DeLong, H.B., Lieffers, V.J. et Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

Doucet, R., 1988. La régénération préétablie dans les peuplements forestiers naturels au Québec. For. Chron. 64: 116-120.

Eis, S. 1967. Establishment and early development of white spruce in the interior British Colombia. For. Chron. 43: 174-177.

Gagnon, R. 1985. Croissance du sapin baumier en relation avec la durée de sa période initiale d'oppression. Mémoire de maîtrise, Université Laval, Québec.

Haeussler, S. et Kneeshaw, D.D. 2003. Comparing forest management to natural processes. *In* Towards sustainable management of the boreal forest: emulating nature, minimizing impacts, and supporting communities. *Édité par* P. J. Burton, C. Messier, D. W. Smith et W. L. Adamowicz. NRC Research Press, Ottawa, Ont. pp. 307-368.

Harman, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Ecol. Res., 15: 133-302, USDA Forest Service.

Hatcher, R.J. 1960. Croissance du sapin baumier après une coupe rase dans le Québec. Direction des forêts. Environnement Canada. Mémoire technique no 87.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1-23.

Hunter, M.L. 1993. Natural disturbance regimes as spatial models for managing boreal forests. Biol. Conserv. 65: 115-120.

Jobidon, R. 1995. Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec. Revue de littérature. Mémoire de recherche forestière no 117. Ministère des Ressources naturelles, Québec. 180 p.

Kneeshaw, D. D. et Bergeron, Y., 1996. Ecological factors affecting the abundance of advanced regeneration in Quebec's south-western boreal forest. Can. J. For. Res. 26: 888-898.

Kneeshaw, D.D. et Bergeron, Y. 1998. Canopy gap caracteristics and tree replacement in the southeastern boreal forest. Ecology, 79(3):783-794

Kneeshaw, D.D. et Burton, P.J. 1997. Canopy and age structures of some old sub-boreal Picea stands in British Columbia. J. Veg. Sci. 8: 615-626.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography and regeneration dynamics of boreal coniferous forest in Finland: a review. Ann. Zool. Fenn. 31: 35-51.

Laflèche, V., Ruel, J.-C. et Archambault, L. 2000. Évaluation de la coupe avec protection de la régénération et des sols comme méthode de régénération de peuplements mélangés du domaine bioclimatique de la sapinière à bouleau jaune de l'est du Québec, Canada. For. Chron. 76(4): 653-663.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, 73: 1943-1967.

Lindenmayer, D.B. et Franklin, J.F. 1997. Forest structure and sustainable temperate forestry: case study from Australia. Conserv. Biol. 11: 1053–1068.

Lindenmayer, D.B. et Franklin, J.F. 2002. Conserving forest biodiversity. A comprehensive multiscaled approach. 351 p. Island Press: Washington, DC.

MacArthur, J. D., 1963. Effect of mechanized logging on the composition of balsam fir stand in the Gaspé Peninsula. Pulp Pap. Mag. Can. 65: WR208-WR210.

MacDonnell, M. R. et Groot, A., 1997. Harvesting peatland black spruce : impacts on advance growth and site disturbance. For. Chron. 73: 249-255.

MacLean, D.A., 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56: 213-220.

MacLean, D.A., 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. 60: 273-279.

MacLean, D.A. et Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can. J. For. Res. 19: 1087-1095.

Marquis, D.A. 1965. Scarify soil during logging to increase birch reproduction. North. Log. 14 (5): 24, 42.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. 9: 1-59.

McRae, D. J., Duchesne, L. C., Freedman, B., Lynham, T. J. et Woodley, S., 2001. Comparisons between wildfire ans forest harvesting and their implications in forest management. Environ. Rev. 9: 223-260.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in th Boreal Zone of Quebec. Can. J. For. Res. 24: 730-741.

Morin, H. et Laprise, D. 1989. Histoire récente des épidémies de la Tordeuse des bourgeons de l'épinette au nord du lac Saint-Jean (Québec): une analyse dendrochronologique. Can. J. For. Res. 20: 1-8.

Morin, H., Laprise, D. et Bergeron, Y., 1993. Chronology of budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. 23: 1497-1506.

Morris, R. F., 1963. The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can. No. 31.

Packee, E.C. 1990. White spruce regeneration on a bladed-scarified Alskan Loess soil. North. J. Appl. For. 7: 121-123.

Parker, V.T. et Pickett, S.T.A. 1998. Historical contingency and multiple scales of dynamics within plant communities. *Dans* D.L. Peterson et V.T. Parker. Ecological scale: theory and applications. Colombia University Press, New York. Pp. 171-192.

Pastor, J., Light, S. et Sovell, L. 1998. Sustainability and resilience in boreal regions: sources and consequences of variability. Conservation Ecology [online] **2**(2): 16. Disponible sur Internet. URL:http://www.consecol.org/vol2/iss2/art16/

Perala, D.A. et Alm, A.A. 1990. Reproductive ecology of birch: a review. For. Ecol. Manage. 32: 1-38.

Ruel, J.-C. 1992. Impact de la compétition exercée par le framboisier (*Rubus idaus* L.) et les feuillus de lumière sur la croissane du sapin (*Abies Balsamea* (L.) Mill.) en régénération. Can. J. For. Res. 22: 1408-1416.
Simard, M.-J., Bergeron, Y. et Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. 9: 575-582.

Ruel, J.-C., Ouellet, F., Plusquellec, R. et Ung, C.-H. 1998. Évolution de la régénération de peuplement résineux et mélangés au cours des 30 années après coupe à blanc mécanisée. For. Chon. 74(3): 428-443.

Webb, L. S., 1961. Clear cutting of pulpwood in the balsam fir spruce forest of Gaspe. Pul Pap. Mag. Can. 62 n° C (Convention Issues): 238-248.

SECTION II: COMPARISON OF THE EFFECTS OF A SPRUCE BUDWORM OUTBREAK TO HARVESTING AND THINNING AT LANDSCAPE AND STAND SCALES

Jonatan Belle-Isle et Daniel Kneeshaw

Groupe de recherche en écologie forestière interuniversitaire

Université du Québec à Montréal

C. P. 888, succursale Centre-Ville, Montréal, Québec

2.1 Abstract

Spruce budworm (SBW) outbreaks are a major disturbance determining boreal forest dynamics in forests dominated by balsam fir. However, anthropogenically, these forests have been disturbed in recent decades by clearcutting with protection of advance regeneration and soils (CPRS) which it has been suggested, emulates SBW outbreaks by leaving a seedling bank while removing the overstory. The main objective of this study is to characterize and compare the effects of a SBW outbreak to the effects of CPRS, in balsam fir stands in the Gaspe Peninsula. The study was conducted at two different scales; the stand scale, by field sampling vegetation, and at the landscape scale, through the interpretation of aerial photographs. At the stand scale, results showed a more important structural variability in stands affected by the SBW outbreak. There was a greater diversity of saplings and trees, especially paper birch and white spruce, in SBW stands by comparison to CPRS stands. At the landscape scale, canopy openings created by CPRS presented less regular shapes, but still had smaller perimeter/area ratio because of their larger size. SBW openings are thus more likely to be influenced by the surrounding forest and recolonisation by tree species should be faster than for CPRS openings. Our results suggest that efforts should be made to preserve associated species (paper birch and white spruce) by preserving more overstory trees of these species while managing the balsam fir dominated forest. Aggregation of cutting units should be limited and there is a need to create more small canopy openings in the landscape if we are to emulate naturally created patterns.

2.2 Introduction

Natural disturbances are now seen as an essential driving force for the maintenance of ecosystem integrity and diversity (Haeussler and Kneeshaw 2003). Currently, several forest management practices are based on understanding and emulating natural disturbances. It has been suggested that management strategies favoring a composition and a structure similar to those characterizing natural environments should allow the maintenance of biodiversity and essential ecosystem functions (Franklin 1993; McKenney et *al.* 1994; Gauthier et *al.* 1996). To guide the emulation of a natural disturbance in management strategies, it is essential to characterize in detail the similarities and differences between logging and associated practices and the relevant natural disturbance. Most research comparing natural and anthropogenic disturbances was conducted on the effects of wildfire versus clearcutting (Haeussler and Kneeshaw 2003). Recent research, however, shows that intermediate natural disturbances are more frequent that we thought in the boreal forest, and in some regions, more important than fire (Kuuluvainen 1994; Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Cumming et *al.* 2000; McCarthy 2001). Spruce budworm (SBW) outbreaks represent, after fires, the most important disturbance affecting boreal forests in eastern Canada (Morin and Laprise 1989; Kneeshaw 2001). Their effects on the structure and composition of these ecosystems should thus be considered in forest management practices aiming to emulate natural disturbances.

The SBW is a native insect of eastern North America that defoliates host trees (i.e. balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.)), and red spruce (*Picea rubens* Sarg.)). Repeated destruction of annual shoots often leads to mortality of host trees since they become unable to produce the necessary resources to survive (Blais 1981; MacLean and Ostaff 1989). Balsam fir over 10 cm DBH (diameter at breast height) usually start dying after 5 years of severe defoliation (75 to 100%) (Belyea 1952; Blais 1958; Batzer 1973) and white spruce after 6 to 7 years (Blais 1981). Mortality is usually complete within 10 years of the beginning of the outbreak (MacLean 1980), although Baskerville and MacLean (1979) have recorded mortality up to 16 years following the beginning of the outbreak.

In contrast to SBW outbreaks, traditional clearcutting destroys an important part of the pre-established regeneration (Weetman 1965). Clearcutting done in Quebec and New-Brunswick without any effort to preserve advance growth allowed survival of only 10 to 30% of small balsam fir and white spruce stems (Frisque et *al.* 1978; Harvey and Bergeron 1989; McInnis and Roberts 1994). Moreover, few coniferous seed trees remain after cutting and their seeds do not scatter over very long distances (Burns and Honkala 1990). Thus, clearcutting alone does not seem to be appropriate to ensure coniferous stand renewal. Therefore, clearcutting is now usually made with an attempt to preserve advance regeneration to shorten the revolution time. This management practice is often called clearcutting with protection of advance regeneration and soils (CPRS in this study). It has been suggested that this method should be sufficient to maintain stands in balsam fir dominated forests, since their structure is fairly homogenous and advance regeneration is often abundant (Hatcher 1960; Ruel et *al.* 1998). In our study area, CPRS is followed by a pre-commercial thinning (PCT) done about ten years following the initial cutting. One of the objectives of this intervention is to control tree species composition by limiting deciduous species invasion. PCT is an integral part of the management practice, altering the regeneration paths of the cut stands to bring its composition closer to the original pre-harvest composition. Since these two practices always occur together on the Gaspe Peninsula, their effects on forest regeneration are combined and thus they were studied as one single disturbance; CPRS+PCT.

Balsam fir regenerates well naturally (Ruel 1992). Its seed production starts early in development and good production years follow at a regular rhythm (Fowells 1965). Its seedlings can survive several years under a closed canopy, and then form an abundant pre-established regeneration (Hatcher 1960; Morin 1994). Even in poor light conditions, balsam fir maintains its capacity to respond to canopy openings, allowing it to replace canopy trees in stands devastated by disturbances such as cutting, windthrow or insects outbreaks, as long as they do not destroy the pre-established fir seedling bank (Gagnon 1985; Ruel 1992). Balsam fir forests are thus well adapted to recurrent SBW outbreaks and CPRS, since these disturbances preserve the pre-established regeneration.

It has thus been suggested that CPRS and severe SBW outbreaks will lead to similar effects on the composition of balsam fir dominated stands (Baskerville 1975; MacLean 1984; Bergeron et *al.* 1999). Major differences in terms of forest structure are, however, expected to occur between these two types of disturbances. The abruptness of the canopy opening created by CPRS allows greater light availability to the forest floor than gradual openings created by the SBW. The SBW also leaves residual trees, snags and coarse woody debris (Lieffers et *al.* 2003) which may not be very abundant following CPRS. These differences should affect the structure and the composition of the stands following either one or the other of these disturbances. Some landscape characteristics are also expected to differ. Canopy openings created by SBW outbreaks are usually small (Kneeshaw and Bergeron 1998) in comparison to cutting units which are often aggregated to form openings larger than 100 ha. The SBW outbreak is then expected to create a fine-scale mosaic where small openings are scattered in the territory, while aggregated cutting units would create a coarser-scale mosaic.

Although it has been suggested that natural disturbances are important for ecosystems variability and integrity (Angermeier and Karr 1994; Pastor et *al.* 1998), forest management practices are thought to reduce stand and landscape level variability (Bergeron et *al.* 1998), which in turn can lead to the system becoming less resilient to disturbance or stress (Holling and Meffe 1996). The main objective of this study is thus to characterize and compare the effects of a natural stand-level disturbance, a SBW outbreak, with the effects of a silvicultural treatment, CPRS+PCT, in balsam fir stands on the Gaspe Peninsula. By characterizing the differences and similarities between these disturbances, it should be possible to evaluate some aspects of the ecological integrity of forests managed with CPRS+PCT. Since forest composition and structure evolve through time following disturbances, stands observed several years after disturbances should provide a good picture of the direction of forest response and thus allow us to evaluate the resilience of the system to CPRS+PCT. This evaluation will also permit us to propose solutions to improve current forest management practices to bring them closer to natural ecosystem processes.

2.2.1 Study area

Our study area is located in the Baie des Chaleurs region of the Gaspe Peninsula, in south-eastern Quebec, and is part of the Nordic temperate and boreal zones (Saucier et *al.* 1998). The total area of the territory under investigation is approximately 3440 Km^2. The landscape is composed of hills, mountains, plateaus and valleys, with summits varying between 300 and 900 m in altitude. Study sites are located in the balsam fir-white birch bioclimatic domain. Balsam fir and white birch (*Betula papyrifera* Marsh.) dominate the canopy while white spruce and black spruce are occasionally found. The mean annual temperature varies between 0°C and 1°C while mean annual precipitation is between 900 and 1200 mm (Saucier et *al.* 1998).

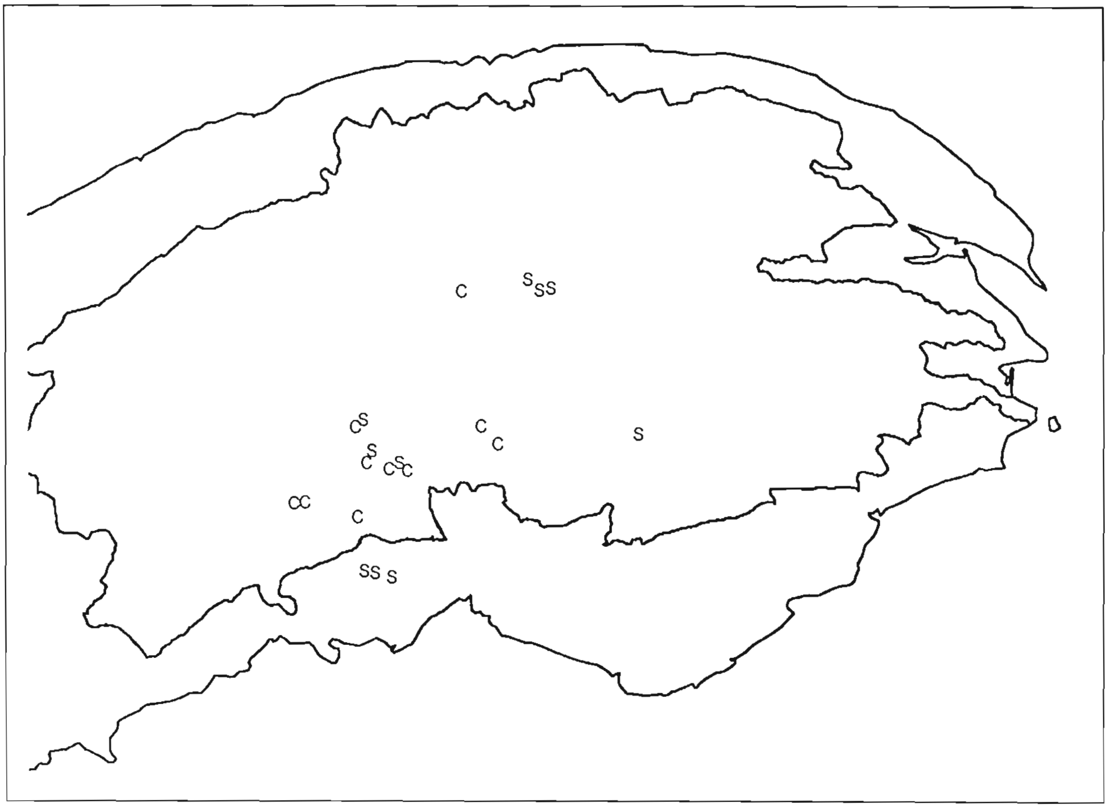


Figure 1. Location of the studied sites (SBW (S) and CPRS+PCT (C)) on the Gaspe Peninsula.

2.3 Methods

For a better understanding of ecosystem processes and responses, this study was conducted at two different scales. The first part of the study was conducted at the stand scale by field sampling vegetation data, aimed to characterize the effects of SBW outbreaks and CPRS+PCT on organic matter abundance such as snags, coarse woody debris, residual trees, and regeneration found after disturbance. The second part was conducted at the landscape scale, through the interpretation of aerial photographs. For this part, we characterized the sizes, shapes and spatial distributions of the openings created by both disturbances.

2.3.1 Field sampling vegetation

At the stand scale, the study took place in coniferous stands dominated by balsam fir, with a light to moderate slope. Ten sites severely affected by the most recent SBW outbreak (1980's) in Gaspesie and 10 CPRS sites cut in 1989 and thinned about 10 years later were sampled during the summers of 2003 and 2004 (Fig. 1). The stands were randomly chosen from ecoforestry maps listing every natural disturbances and management practice conducted by the forest industry Temrex. The age and the height of the stands prior to disturbance were also verified on older ecoforestry maps to ensure that stands affected by the different disturbances were comparable. In CPRS stands, the year of the PCT was evaluated in the field by determining the age of sprouts originating from the stumps of non commercial deciduous trees and shrubs removed by the PCT.

In each CPRS+PCT stand, twelve to fifteen 100 m^2 plots were randomly established while three to six 100 m^2 plots were established in SBW outbreak openings (fewer plots were placed in SBW sites because the area affected was usually much smaller than disturbances caused by CPRS+PCT). In both disturbance types, plots were distanced by at least 20 m from each other, and 30 m from roads and edges (i.e. with openings or other stand types). All trees 7 cm DBH and over (class 6) were measured in every 100 m^2 plot. In one half of each plot (50 m^2), saplings between 4 and 6.9 cm DBH (class 5) were measured. Mortality caused by the 1989 CPRS and the latest SBW outbreak was measured by censusing snag and uprooted trees (over 7 cm DBH) for both disturbances, and stumps for CPRS in every 50 m^2 plot. Mortality caused by the PCT was measured by censuring small cut stumps (less than the commercial tree size of 9.1 cm DBH), clearly distinctive from those created by the CPRS, in every 10 m^2 plot. Arboreal regeneration less than 4 cm DBH were divided into four classes: **1-** 1 to 9.9 cm in height, **2-** 10 to 99.9 cm, **3-** 1 to 1.99 m, and **4-** 2 m in height and < 4 cm DBH. Density of each species was evaluated for each one of these 4 size classes. Relative density was calculated for each species in relation to the total density of all woody species in each size class. Sampling effort for these 4 vegetation classes within each 100 m^2 plot was a function of abundance of each species in each class, varying from 3 m^2 to 100 m^2. Lateral cover was visually estimated for each tree species in each class as well as for invasive species such as raspberries (*Rubus idaeus* L.), ferns (*Dryopteris spinulosa* (O. F. Muell.) Watt, *Dryopteris Phegopteris* (L.) C. Chr., *Dryopteris disjuncta* (Ledeb.) Morton) and fire weed (*Epilobium angustifulium* L.). Coarse woody debris over 7 cm of diameter were measured in each plot using the line-intercept sampling method (Warren and Olsen 1964; Van Wagner 1968). Their decomposition state was evaluated using a deterioration key (Imbeau and Desrochers 2002).

The recent SBW outbreak on the Gaspe Peninsula occurred from the late 1970's until mid 1980's. The peak of mortality caused by the outbreak occurred in 1982, but the trees probably continued dying for several years (MacLean 1980). There was thus a small delay between the creation of the openings caused by the SBW and those caused by the 1989 CPRS observed for this study. Earlier CPRS could not be observed since this type of management started in 1988 on the Gaspe Peninsula, and only a few CPRS was made during that year. Total canopy openings (less than 25% remaining canopy cover) of stands affected by severe defoliation probably appeared during the second half of the 1980's, so the time delay between both disturbances observed for this study was not so great.

To minimize wood loss caused by the SBW outbreak, there has been a wood recovery harvest after the outbreak. The stands selected for the study were not subject to any wood recovery harvest either because there was no road access at that time or because they were not identified on the ecoforestry maps used by the forestry industry to make these recovery harvests.

2.3.2 Interpretation of aerial photographs

At the landscape scale, canopy openings (less than 25% remaining canopy cover) created by severe SBW defoliation were studied through the interpretation of aerial photographs. Four sets of 1:15000 aerial photographs taken during the summers of 1993 or 1994 were randomly chosen among coniferous stands dominated by balsam fir and not affected by logging. Openings were delimited onto an acetate overlaid onto each aerial photograph, scanned, and analyzed using "Xtools", an Arc View extension, to obtain perimeter and area for each opening. A total area of 27.74 Km^2 was observed on aerial photographs. Openings created by CPRS between 1988 and 1998 in balsam fir dominated stands were also analyzed with "Xtools", using ecoforestry maps as a reference. A total area of 3483 Km^2 was evaluated on these maps to obtain a comparable amount of openings for the two types of disturbances.

2.3.3 Data analysis

At the stand scale, the richness and the Shannon-Wiener diversity index (Stiling 1996) were calculated for each size class. Horizontal structural heterogeneity was evaluated by using the absolute density variance of each size class in each stand. These variables were compared between stands following the SBW outbreak and stands following CPRS+PCT compared using ANOVA. Mean densities of snags, stumps and uprooting trees were calculated for each site. Means obtained from SBW sites and CPRS+PCT sites were than compared using ANOVA. The same method was use to compare coarse woody debris characteristics (density, diameter, volume, and deterioration state). The ANOVAs were performed with JMP. Data were transformed when needed.

Vegetation data used for the analysis of compositional differences and their relationship to environmental variables consist of relative density for each size class of each species. Environmental data consist of the type of disturbance, snags density, and coarse woody debris volume. CANOCO (ter Braak and Smilauer 1998) was used to perform a redundancy analysis (RDA) to examine the relationship between vegetation variables and environmental variables (type of disturbance, snags density and CWD volume). This analysis was use to reveal associations between disturbance type (SBW outbreak or CPRS+PCT) and tree species of different size classes. Monte Carlo permutation tests (ter Braak and Smilauer 1998) for the first all canonical axes were performed to detect the significance of the RDA.

At the landscape scale, shapes, sizes and spatial distribution of canopy openings created by both disturbances were observed. Shapes were characterized by the ratio perimeter/area and a regularity index. The regularity index use for this study is the proportion of the perimeter of the measured opening to the minimal perimeter that an opening of the same area would have if it was perfectly circular.

$$\text{Regularity index} = \frac{\text{minimal perimeter}}{\text{measured perimeter}}$$

A higher regularity index indicates a more regular shape, i.e. closer to a circular shaped opening. Mean area was used to characterize sizes, and distance from the closest opening created by the same disturbance was used to characterize spatial distribution. These variables were compared by ANOVA.

2.4 Results

2.4.1 Stand scale

Mortality

Even though some mortality on CPRS+PCT sites was not caused directly by forest management, logging was the major disturbance element, causing 86 % of the observed mortality. The SBW outbreak left some mature trees as large as 37 cm DBH in the affected stands, mostly white spruce and white birch (Fig. 2). In contrast, trees found in stands following CPRS+PCT were all under 16 cm DBH fifteen years after logging, except for one birch over 7 cm DBH. Dead trees that could not be identified because of their late stage of deterioration (Table 1) probably originated from the period preceding the one affected by the latest SBW outbreak.

Table 1. Mean snags, uprooted trees and stumps densities (stems/ha) fifteen years after a SBW outbreak and CPRS+PCT.

	SBW			CPRS+PCT			
	snags	uprootings	total	stumps	snags	uprootings	total
conifers	1298	421	1718	1472	27	199	1698
white birch	21	12	33	35	3	20	58
unidentified	46	23	68	0	0	4	4
total	1364	455	1820	1507	30	216	1754

Vegetation cover and regeneration

Some elements affecting light condition on the forest soil differed between postoutbreak and postlogging stands. A few residual trees (> 15 cm DBH) (Fig. 2) and a lot of snags (Table 1) were left by the SBW outbreak. Saplings and trees (size classes 5 and 6) densities (Fig. 3) as well as their crown cover (Fig. 4) were more important on SBW sites. The PCT done about 10 years following the CPRS eliminated a mean of 37772 stems/ha, of which 68% were balsam fir and 20% white birch, allowing more light to reach ground level. All deciduous species sprouted back following thinning, with a mean proportion of 81.2% of total deciduous cut stems. A lot of other small deciduous stems observed in CPRS+PCT stands probably emerged with the reduction of vegetation cover following thinning. Subsequently, the small regenerating tree classes (size classes 1 to 4) were mostly composed of shade intolerant species on CPRS+PCT sites while many more shade tolerant regenerating tree species were found on SBW sites (Fig. 5). Biplots obtained from redundancy analyzes (RDA) performed on the relative densities of small regeneration (size classes 1 to 4) (Fig. 6) shows that regenerating shade intolerant species such as white birch and pin cherry (*Prunus pennsylvanica* L.f.) are mostly associated with CPRS+PCT, while balsam fir, a shade tolerant species, is closely associated with the SBW outbreak. The first and the second axis explained 59.2 and 1.9% (respectively) of the variation observed in the vegetation data. Disturbance type was revealed to be very important for the variation in species relative density, with a correlation coefficient of 0.78 with the first species axis, and 0.19 with the second. Monte Carlo tests for the first and all canonical axes shows that environmental variables significantly affected regeneration relative density (F=23.2, p=0.005; F=8.47, p=0.005, respectively). Invasive species such as raspberries, ferns and fire weed which are often found in postfire or postlogging stands where sunlight is high were also more abundant on CPRS+PCT sites, with 2.27 % cover, compared to 0.70 % on SBW outbreak sites. The ANOVA showed that this difference is significant, although cover by these invasive species was not very important fifteen years after disturbance.

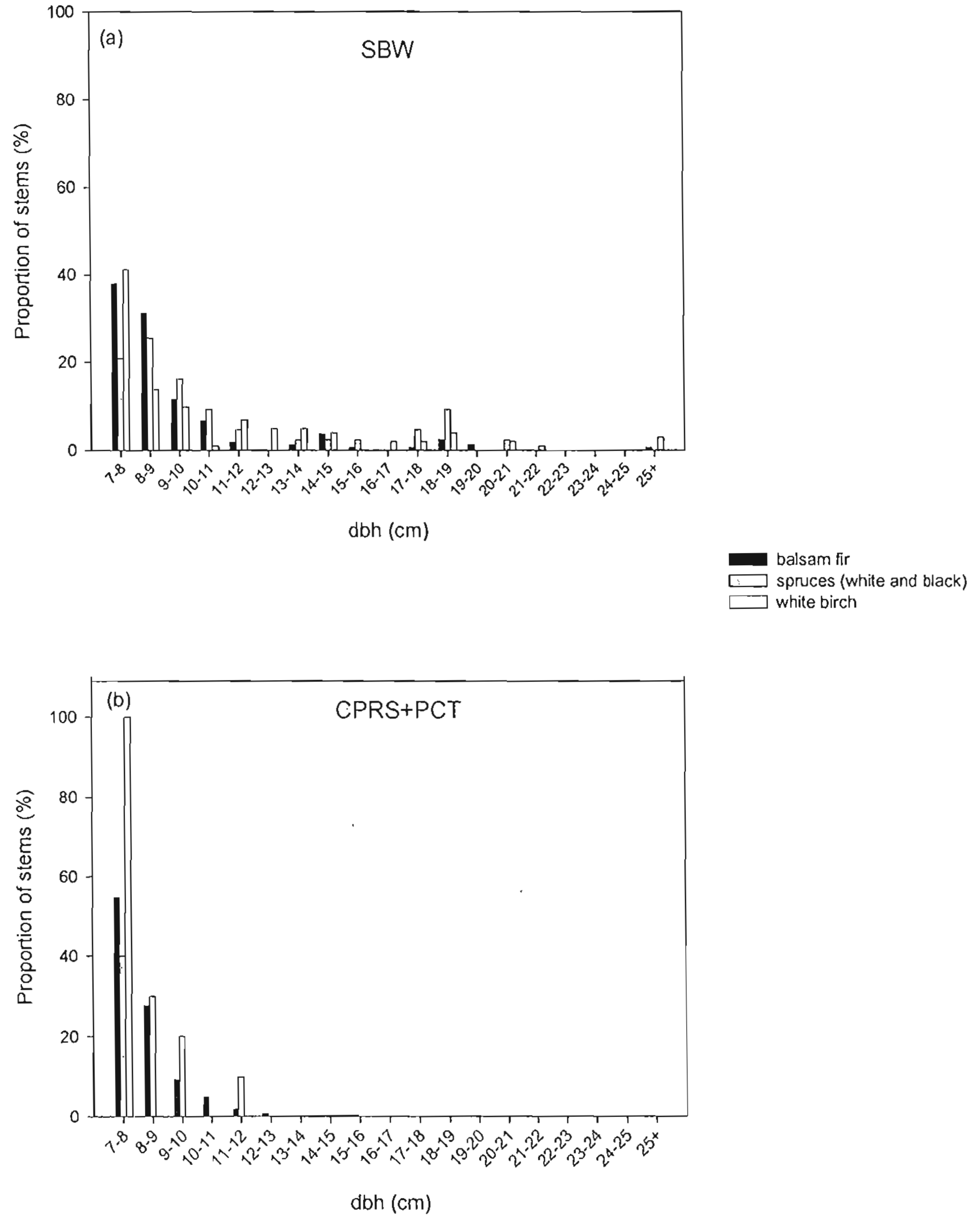


Figure 2. Diameter distributions of mature balsam fir, spruces and white birch following the SBW outbreak (a) and CPRS+PCT (b). Proportions were calculated for each species as the number of trees in a DBH class relative to the total number of trees.

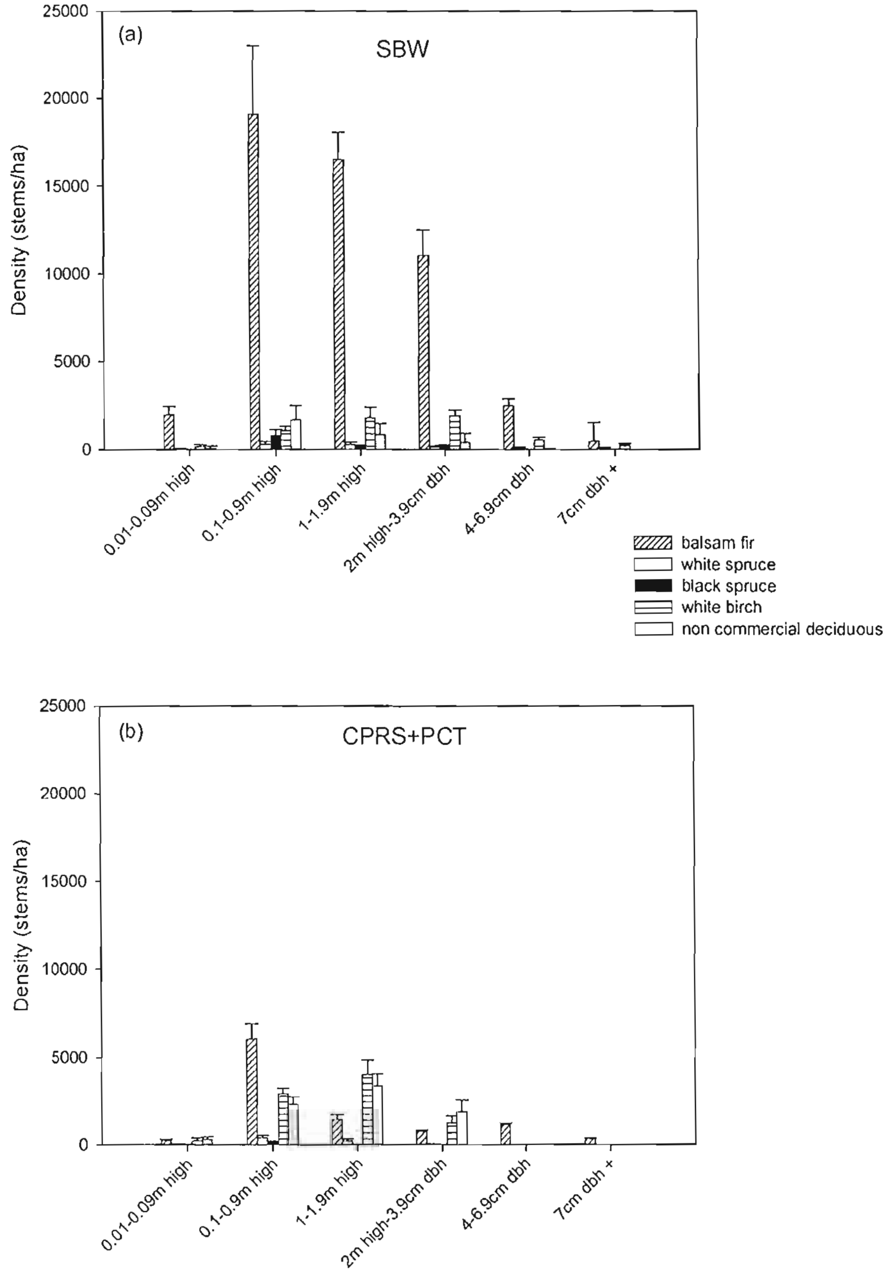


Figure 3. Density of four regeneration classes (classes: **1-** 1 to 9.9 cm of height, **2-** 10 to 99.9 cm, **3-** 1 to 1.99 m, and **4-** 2 m of height and < 4 cm DBH), saplings (**5-** from 4 to 6.9 cm DBH), and trees (**6-** 7 cm DBH and over), for tree species found in stands following (a) the SBW outbreak and (b) CPRS+PCT.

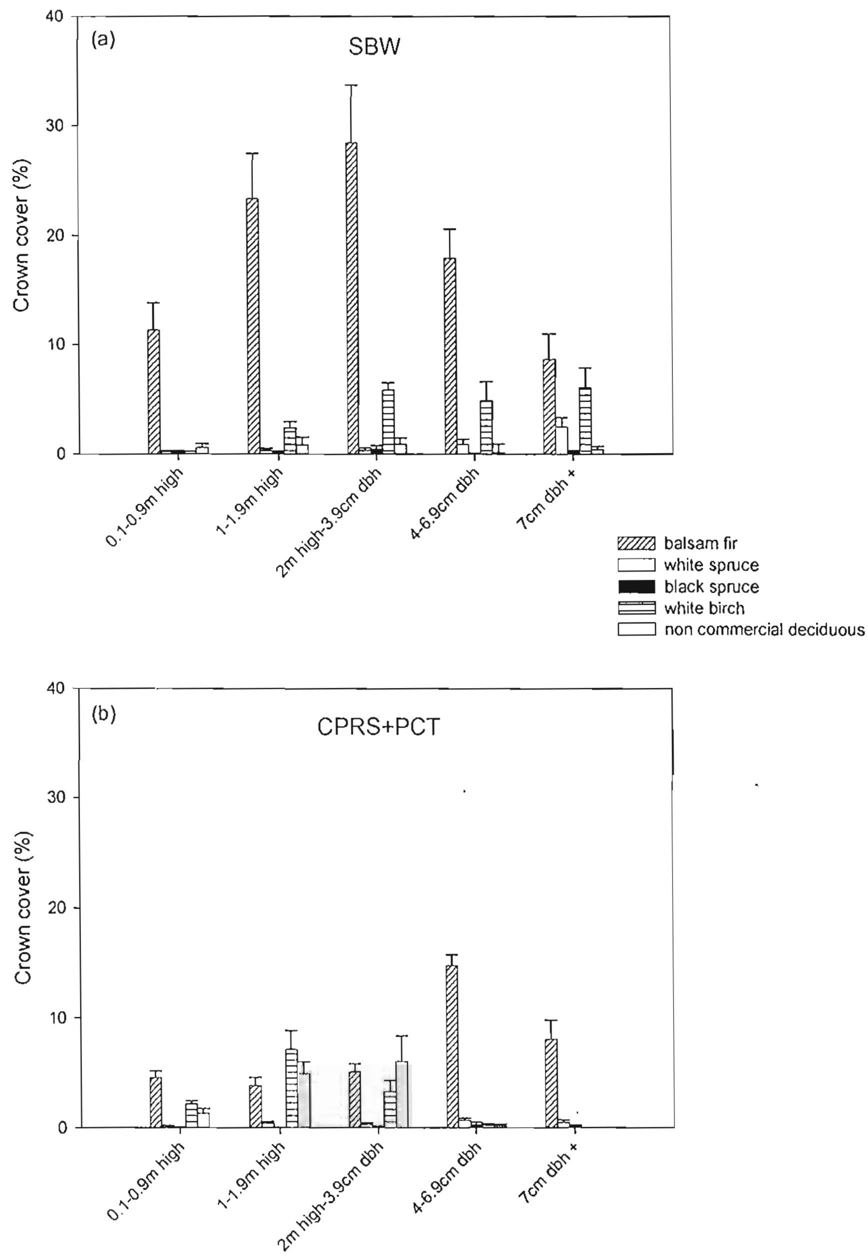


Figure 4. Crown cover of three regeneration classes (2- 10 to 99.9 cm, 3- 1 to 1.99 m, and 4- 2 m of height and < 4 cm DBH), saplings (5- from 4 to 6.9 cm DBH), and trees (6- 7 cm DBH and over), for woody species found in stands following (a) the SBW outbreak and (b) CPRS+PCT.

Tree diversity

Even though a lot of shade intolerant regenerating tree species are found after CPRS+PCT, an important proportion of regenerating balsam fir occurs on these sites (Fig. 5b). Regeneration (classes 1 to 4) following CPRS+PCT is more heterogeneous than in stands following the SBW outbreak where the smaller strata are totally dominated by balsam fir (Fig. 5a). The Shannon-Wiener diversity index for classes 2, 3 and 4 (Table 2), is significantly higher for CPRS+PCT sites than for SBW sites. Richness is also significantly higher in CPRS+PCT stands for classes 2 and 3. On the other hand, sapling and trees are more diverse in the SBW stands which contain a considerable portion of white birch in classes 5 and 6, and a few white spruce in class 6 (Fig. 5a), while saplings and trees in CPRS+PCT stands are almost exclusively composed of balsam fir (Fig. 5b). The RDA done on sapling and tree relative densities associated the SBW outbreak to white birch in classes 5 and 6 and white spruce in class 6, while CPRS+PCT were associated to balsam fir in classes 5 and 6 (Fig. 7). The eigenvalues for the first two axes are 0.546 and 0.021, corresponding respectively to 54.6 and 2.1% of the variation observed in the vegetation data. The Monte Carlo tests for the first and all canonical axes show that environmental variables significantly affected sapling and tree relative density ($F=19.3$, $p=0.005$; $F=7.07$, $p=0.01$, respectively). Shannon-Wiener indices for these classes (5 and 6) are higher for stands following the SBW outbreak (Table 2), but not significantly different for class 5. More mature tree species (class 6) were found after the SBW outbreak than after CPRS+PCT.

Table 2. Comparison of richness and Shannon-Wiener diversity index of each size class for stands following the SBW outbreak and stands following CPRS+PCT, and probabilities obtained from the ANOVA. DF = 18.

	Richness				Shannon-Wiener index			
Size classes	SBW	CPRS+PCT	Prob	F ratio	SBW	CPRS+PCT	Prob	F ratio
1- 0.01-0.09m	1.60	1.80	0.7676	0.0900	0.382	0.715	0.2699	1.1257
2- 0.1-0.9m	4.80	7.50	0.0027	12.1275	0.956	1.917	<.0001	47.447
3- 1-1.9m	4.50	7.10	0.0006	17.1864	0.903	1.822	<.0001	58.356
4- 2m-3.9cm dhp	4.40	5.60	0.0551	4.2078	1.009	1.630	0.0024	12.507
5- 4-6.9cm dhp	3.20	3.20	1.0000	0.0000	0.886	0.540	0.0615	3.9757
6- 7cm dhp +	3.20	2.10	0.0411	4.8400	1.073	0.382	0.0034	11.339

Structure or Variability

Post-outbreak and post-logging stands presented some differences in vertical structural elements. Residual trees and snags, as mentioned earlier, were abundant on SBW sites, and almost absent on CPRS+PCT sites (Fig.2 and Table 1). Coarse woody debris (CWD) was also much more abundant and larger on SBW sites (Table 3). Woody species horizontal heterogeneity was evaluated by using the absolute density variance of each size class in each stand (Table 4). Stands following the SBW outbreak present a significantly greater mean variance for densities of stems of 2 m tall and higher (classes 4, 5 and 6), but no difference was detected in the lower stratum (classes 1, 2 and 3).

Table 3. Coarse woody debris characteristics (mean number on a 10 m linear transect, mean diameter, mean volume, and mean deterioration state (Imbeau and Desrochers 2002)) for stands following the SBW outbreak and stands following CPRS+PCT and probabilities from the ANOVA. DF = 18.

	number/10m	diameter (cm)	volume (m^3)	deterioration
SBW	9.983	14.338	0.026	10.719
CPRS+PCT	3.650	12.469	0.008	10.714
Prob	< 0.0001	0.0044	< 0.0001	0.9143
F ratio	54.805	7.882	63.095	0.0119

Table 4. Horizontal variances for each size class for stands following the SBW outbreak and stands following CPRS+PCT, and the probabilities obtained from the ANOVA. DF = 18.

Size classes	SBW	CPRS+PCT	Prob	F ratio
1- 0.01-0.09m	0.133	0.079	0.4457	0.0680
2- 0.1-0.9m	5.194	0.591	0.2391	1.4827
3- 1-1.9m	2.039	0.361	0.1987	1.7809
4- 2m-3.9cm dhp	0.753	0.107	0.0494	4.4411
5- 4-6.9cm dhp	0.034	0.004	0.0105	8.1671
6- 7cm dhp +	0.004	0.001	0.0444	4.6696

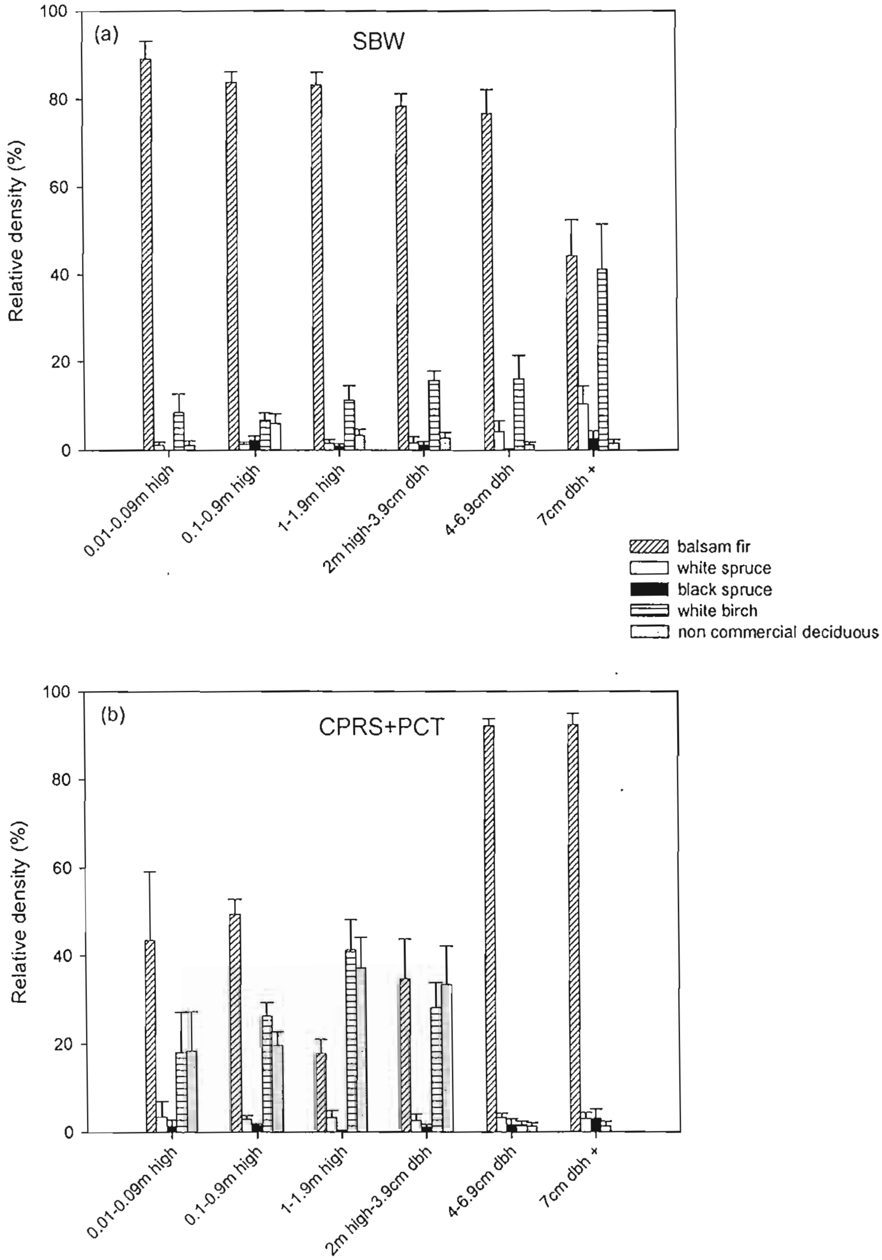


Figure 5. Percentage density of four regeneration classes (classes: 1- 1 to 9.9 cm of height, 2- 10 to 99.9 cm, 3- 1 to 1.99 m, and 4- 2 m of height and < 4 cm DBH), saplings (5- from 4 to 6.9 cm DBH), and trees (6- 7 cm DBH and over), for tree species found in stands following (a) the SBW outbreak and (b) CPRS+PCT.

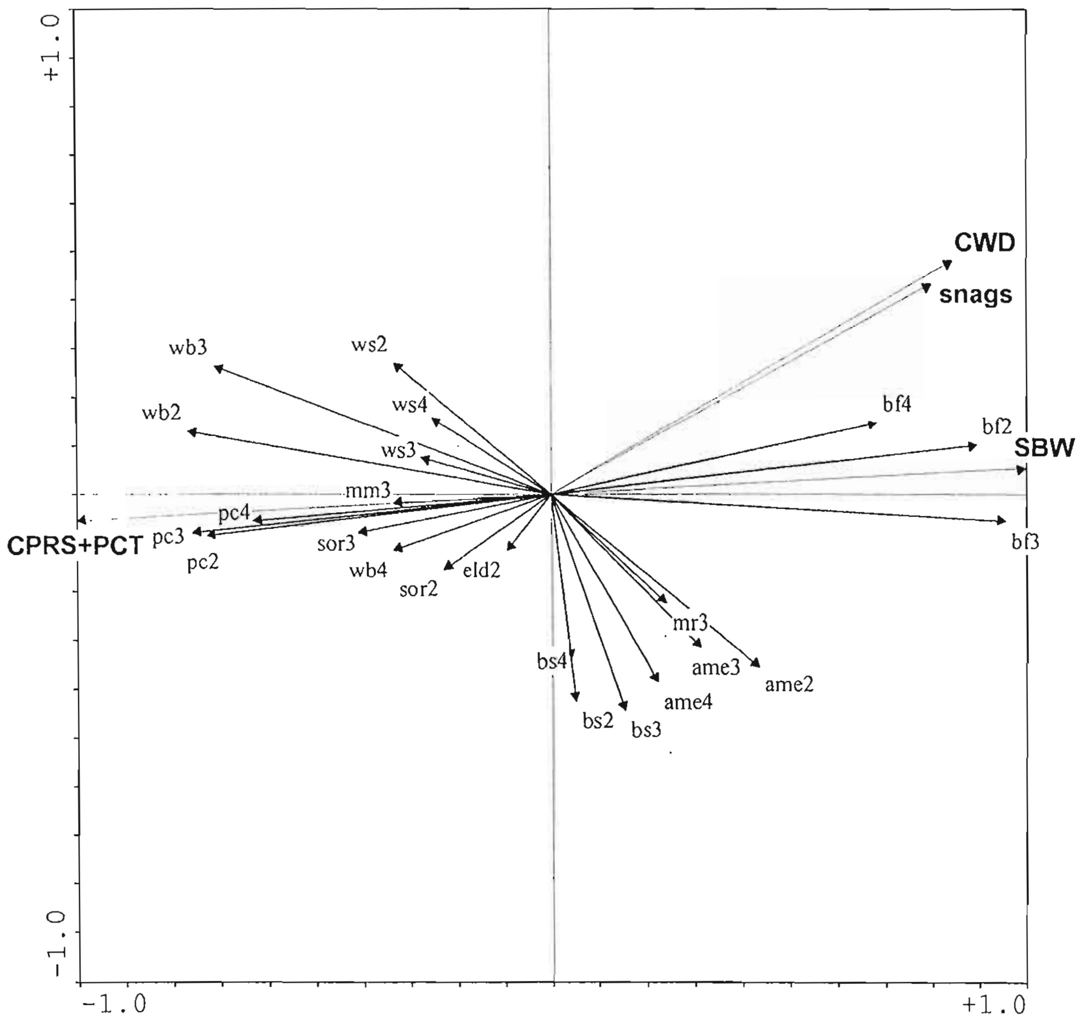


Figure 6. RDA biplot of young regeneration (from 1cm in height to 4 cm DBH) relative densities and environmental variables (type of disturbance (SBW and CPRS+PCT), snags density, and coarse woody debris (CWD) volume). Short forms are as follows: bf = balsam fir, ws = white spruce, bs = black spruce, wb = white birch, mr = red maple, ta = aspen poplar, pc = pin cherry, sor = sorbus spp., mm = mountain maple, eld = eldberry spp., ame = amelanchier spp., and ha = beaked hazel.

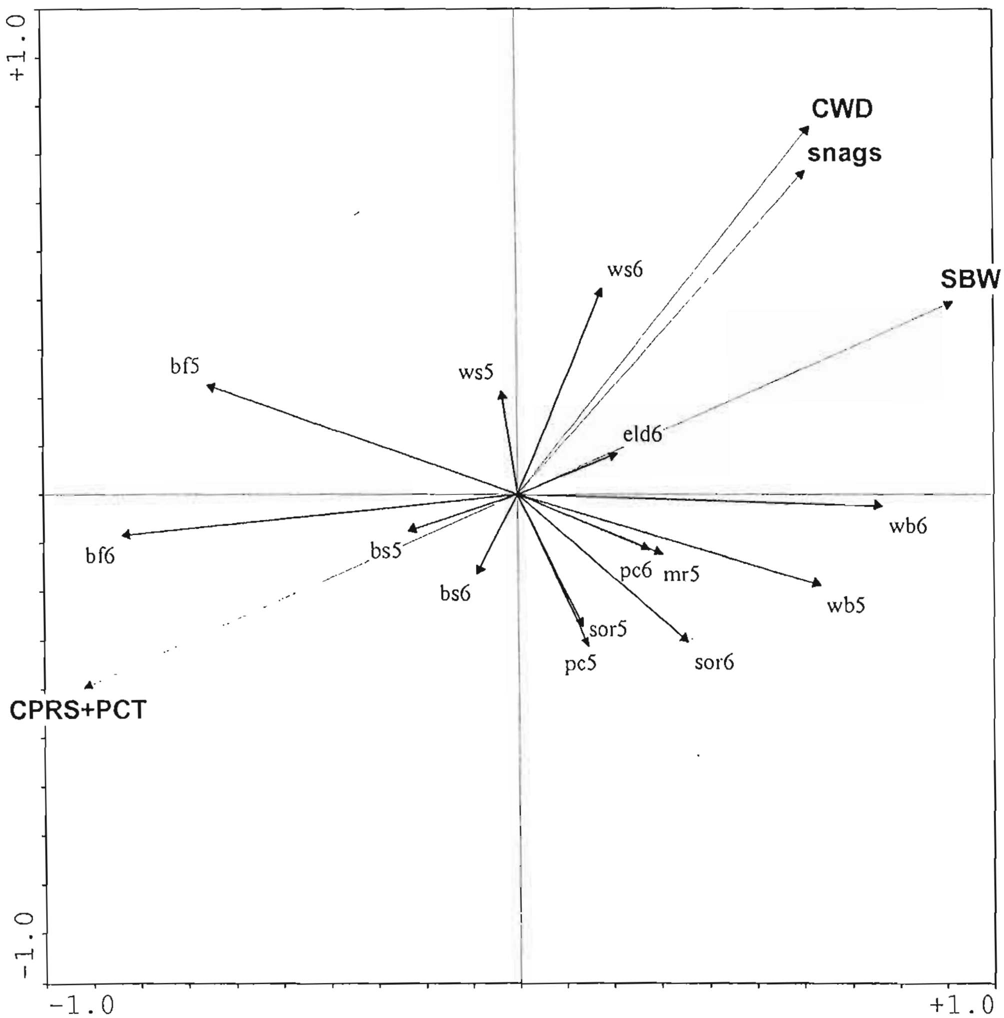


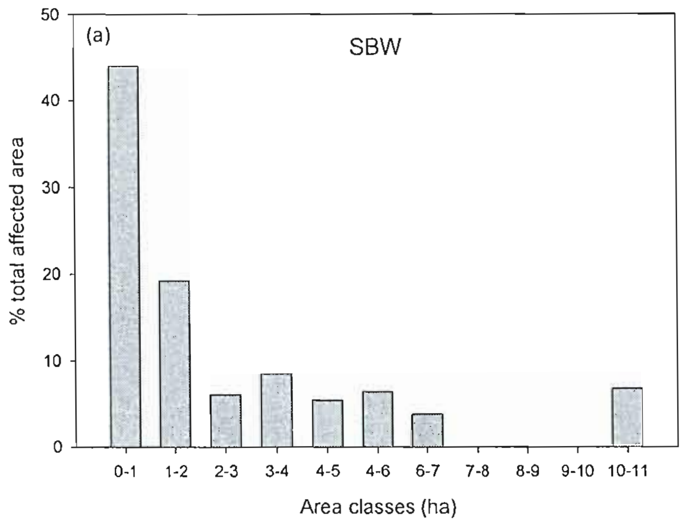
Figure 7. RDA biplot of saplings (from 4 cm to 6.9 cm DBH), and trees (7 cm DBH and over) relative densities and environmental variables (type of disturbance (SBW and CPRS+PCT), snags density, and coarse woody debris (CWD) volume). Short forms are as follows: bf = balsam fir, ws = white spruce, bs = black spruce, wb = white birch, pc = pin cherry, sor = sorbus spp., eld = eldberry spp..

2.4.2 Landscape scale

Results indicate that mean opening area created by CPRS+PCT is about 200 times larger than those created by the latest SBW outbreak, but both disturbances affected a similar proportion of the landscape (table 5). The territory affected by the SBW outbreak is mostly (63%) moulded by opening smaller than 2 ha, and has no opening larger than 11 ha (Fig. 8a). In contrast, nearly all the cut area is made of openings larger than 10 ha, of which an important proportion (29%) is represented by openings larger than 1000 ha (Fig. 8b). Mean distance between openings created by the outbreak is shorter than the mean distance between openings created by logging. SBW outbreak openings are then scattered in the landscape while cut openings are aggregated and separated only by narrow 20m bands of residual living trees. In contrast to our hypothesis, openings created by SBW outbreak tend to have more regular shapes than those created by logging. The perimeter/area ratio though, is higher for SBW openings.

Table 5. Characteristics (mean area, regularity, crossing distance and distance from the next of opening) of canopy openings created by the SBW outbreak and CPRS+PCT, proportions of the territory affected by each disturbance, and probabilities obtained from the ANOVA.

	Area (ha)	Regularity (%)	Perimeter/Area	Distance to next (m)	Affected territory (%)
SBW	0.33	71.53	0.17	37.35	5.99
CPRS+PCT	69.27	54.36	0.03	174.50	6.40
Prob	<0.001	<0.001	<0.001	<0.001	0.884
F ratio	64.07	61.43	887.0	18.37	0.024



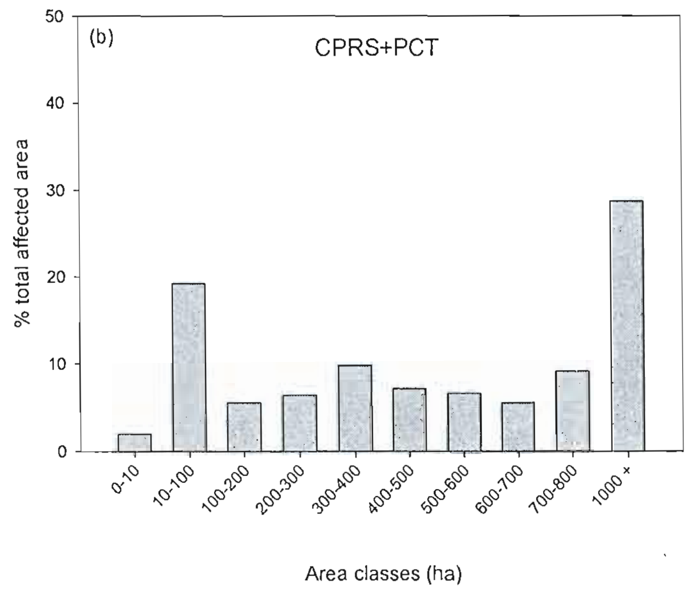


Figure 8. Proportion of the total area affected (a) by the latest SBW outbreak, and (b) by CPRS+PCT done between 1988 and 1998, distributed by classes of size of canopy openings.

Briefly, important differences occur between stands following the SBW outbreak and stands following CPRS+PCT, but there are also some major similarities. Both disturbances caused similar total mortality in mature trees (Table 1), and destroyed similar proportion of the forest canopy (Table 5). On the other hand, regenerating stands present much more heterogeneity following the SBW outbreak. Biological legacies such as coarse woody debris (Table 3), snags (Table 1), and residual trees (Fig. 2) found after the SBW outbreak, create stand complexity that is not found after CPRS+PCT. Besides, variance in stand densities is higher following the SBW outbreak (Table 4). Regenerating stands from CPRS+PCT present more richness and diversity (Table 2), with more deciduous trees in the lower strata, while small regeneration in SBW stands is almost exclusively balsam fir (Fig. 5 and 6). Sapling and trees though, are totally dominated by balsam fir on CPRS+PCT sites, while SBW sites contain a considerable proportion of associated species, i.e. white birch and white spruce (Fig. 5 and 7).

2.5 Discussion

2.5.1 Stand scale

Tree level legacy

Species associated with balsam fir such as white spruce and paper birch were favored by the latest SBW outbreak, but not by CPRS+PCT. Even if white spruce is sensitive to herbivory by the SBW, it is much less vulnerable than balsam fir (Nealis and Régnière 2004), so its mortality rate is lower (Blais 1981). White birch, as a non-host hardwood species, is not affected directly by the SBW. Subsequently, it was not surprising that large white spruce and white birch trees were found after the outbreak (Fig. 2a). These species usually increase in relative abundance in balsam fir dominated stands following SBW outbreaks (Baskerville 1960; Holling 1973), and in our study, a considerable proportion of saplings and trees (classes 5 and 6) of these two species were found in stands following SBW (Fig. 5a) in comparison with stands following CPRS+PCT where the sapling and tree layer is totally dominated by balsam fir (Fig. 5b). The RDA analysis showed that depending on their vulnerability to the SBW, large tree species are associated to different extents to this environmental variable (SBW outbreak) rather than being associated with CPRS+PCT (Fig. 7). In other words, the more vulnerable a species is to the SBW, the lower is its relative abundance following the outbreak in comparison to its abundance following CPRS+PCT. Since the dominant species (balsam fir) is the most vulnerable, the SBW was important in maintaining associated species (paper birch and white spruce).

Regeneration and diversity

It has been shown that SBW outbreaks are gradual, i.e. that mortality occurs over several years, and is generally complete within 10 years (MacLean 1980). This gradual mortality combined with the presence of live residual trees and snags in post-mortality stands creates shady conditions that is less favorable to the growth of intolerant species in the lower stratum (Fig. 5a). In contrast, the high light found after CPRS+PCT, promoted the survival and growth of several deciduous species (Fig. 5b), creating more richness and diversity (Table 2). Other studies have suggested that this deciduous invasion will be temporary (Ruel et *al.* 1998; Porter et *al.* 2004) as most of this regeneration is shade intolerant and will die when the canopy closes over it. Despite a reduced shade tolerant seedling bank resulting from this invasion of deciduous intolerants, the density of fir seedlings may still be sufficient to ensure the formation of a subsequent balsam fir stand. However, there may not be enough seedlings to ensure the return of paper birch and white spruce. These species are not abundant in the canopy following CPRS+PCT (Fig. 5b), and their recruitment in the next generation may be a problem since they mostly regenerate on coarse woody debris and disturbed mineral soil (Marquis 1965; Eis 1967; Packee 1990 ; Simard et *al.* 1998). Skid tracks found after CPRS+PCT may not be sufficient to ensure good seedling establishment (Laflèche et *al.* 2000). In contrast, the presence of large paper birch and white spruce in SBW stands (Fig. 2a) provide seed sources for these species, while the abundant coarse woody debris (Table 3) constitute good germinating beds. These biological legacies should allow for the return of these associated species, and thus favor the maintenance of tree diversity in stands following the SBW outbreak.

Composition

When compared to wildfire, it has been reported that logging generates important changes in species composition such as increases in fir and deciduous species abundance (Boivin 1977; Yang and Fry 1981; Carleton and MacLellan 1994; Haeussler and Kneeshaw 2003). However, authors differ on the direction that this change will take. Harvey and Bergeron (1989) observed a significant shift in dominance from advance softwood regeneration to a mixedwood situation following harvesting. In contrast, Laflèche et *al.* (2000) suggest that management practices often lead to the loss of the deciduous component in mixed stands. White birch, which reproduces well by spouting (Perala 1974; Jobidon 1995), can be expected to regenerate abundantly after cutting, which we observed after the 1989 CPRS (Fig 5b). However, most of these individuals were later removed by the PCT, and birch is thus almost absent from the canopy after this treatment (Fig. 5b). Even though the stems cut during the thinning sprouted back to form an abundant regeneration layer of white birch, most are in the understory and there is a doubt that many will reach the canopy.

It has been suggested that SBW outbreaks result in the forest shifting back and forth between birch and fir dominance (Marchand 1990). This shifting in dominance seems to be more likely in southern mixedwood forests where birch is more abundant. In balsam fir dominated stands, SBW outbreaks seems only to permit for the persistence of white birch (Holling 1973) but not its dominance.

Structure and variability

Snags and coarse woody debris are much more abundant, and larger following a SBW outbreak than after CPRS+PCT (Tables 1 and 3). Added to live residual trees (Fig. 2), these elements create vertical structural heterogeneity in the regenerating stand, and provide habitats for vegetative and animal species that depend on these forest components (Harman et *al.* 1986).

In postlogging stands, lower densities of live trees in every size classes (Fig 3), and lower variability in density for stems over 2 m high (Table 4) were probably caused by the PCT that homogenizes densities throughout the cut stands. This practice is thus responsible for important structural differences between CPRS and SBW stands. As suggested by Holling and Meffe (1996), natural resource management should strive to retain critical types and ranges of natural variability in ecosystems. Accordingly, reducing natural oscillations through management practices would lead to the system becoming less resilient to disturbance or stress.

2.5.2 Landscape scale

Opening size and regularity determine the importance of edge effects (Bradshaw 1992). Irregular shaped openings are usually expected to be subject to edge effects more than regular shaped openings, but this is not the case here. Even though openings created by the SBW outbreak are more regular then openings created by CPRS+PCT, they still have more edges per area unit because they are much smaller (Table 5).

The size of canopy openings is one of the major differences observed between the effects of the most recent SBW outbreak and the 1989 CPRS+PCT. Openings created by these disturbances are on different scales that overlap only a little (Fig. 8). At the landscape scale, harvesting created a greater and more persistent degree of opening than SBW outbreaks. Since both disturbance affected similar proportions of the forest, we can assume that the SBW outbreak created more, but smaller openings than CPRS+PCT. The natural disturbance thus resulted in a fine-scaled mosaic by comparison to the coarser-scaled mosaic created by CPRS+PCT.

The species composition of the regeneration phases is largely determined by the size of the opening (Liu and Hytteborn 1991). Small openings which are dominated by edge effects, do not favor the growth of intolerant species as much as large openings. In our study, we observed that larger openings created by CPRS+PCT favored the growth of more light demanding-species (Fig. 6), increasing the diversity of the small regenerating stems in CPRS+PCT stands (Table 2). This is in agreement with Runkle (1982) who observed greater diversity in larger forest openings. As mentioned above, stand level characteristics following the two disturbances investigated also lead to these same differences in composition and diversity. The importance of the edge effects following the SBW outbreak is then combined with the slower stand level mortality and the presence of snags and residual trees to provide shady conditions that limits the growth of intolerant species. By contrast, the large size of the canopy openings created by CPRS+PCT is combined with the abruptness of the stand level mortality and the absence of residual tree to provide intense light conditions that favor the growth and survival of intolerant species. These positive feedbacks between stand and landscape scale accentuate and clarify the differences between forests affected by the SBW outbreak and forests managed with CPRS+PCT. PCT attempts to balance some of the compositional differences by favoring balsam fir in CPRS stands although our study suggests that important compositional differences still persist.

2.6 Management implications

PCT following CPRS or other total cuts has often been reevaluated recently. It seems that this practice may lead to the loss of snags and coarse woody debris, the elimination of mixed species composition and biodiversity that these features support (Bergeron et *al.* 1995; Larson and Danell 2001). However, PCT may represent one of the key steps for ecosystem-based management. CPRS seems to favor shade intolerant species by creating large openings with very few snags and residual trees, although PCT favors the dominance of balsam fir to a point that it dominates the canopy layer of these stands. Without PCT, deciduous species such as white birch would grow back successfully, and its strong competition with conifers would reduce the productivity of these more desirable species. Regarding white spruce, its abundance following CPRS is probably compromised with or without PCT since seedbeds and seed trees necessary for the establishment of this species are reduced or eliminated. Favoring balsam fir associated species by a selective PCT could increase their abundance in postlogging stands, and bring stands composition closer to what is found in natural ecosystems, while allowing a good productivity of desirable species. The use of this technique helps lead to a more natural composition but leaving some mature birches and spruces in the stands could also favor their return after cutting, while creating the same kind of vertical structural variability found after a SBW outbreak. This tree retention would also favor the presence of other important structural elements such as snags and coarse woody debris which favor the recruitment of many plant species and provide habitat and food source for the fauna (Storer et *al.* 1979; Harman et *al.* 1986; Hunter 1990; McComb and Lindenmayer 1999). Aggregation of cutting units should be limited to get more small canopy openings in the landscape, and thus create uneven-aged landscapes such as those found following a SBW outbreak. Episodic aspect and the different degrees of severity should also be considered in the elaboration of forest management practices inspired by SBW outbreaks.

2.7 Conclusion

Our results related to the SBW outbreak are in agreement with the hypothesis proposed by Holling (1973) that recurrent SBW outbreaks are responsible for the persistence of spruce and birch in balsam fir dominated stands, species that otherwise would be excluded by competition. Fluctuations in the system allow successive forest regeneration to be replaced in such a way that ensures a continual food source for future generations of the SBW (Baskerville 1975). The periodic component that creates these fluctuations is thus essential for the maintain of the SBW and its natural enemies, as well as its host species and their associated species. Even though it is possible to recreate the structure and composition of forests affected by a severe SBW outbreak through silvicultural techniques, it might be much harder to reproduce the processes occurring naturally and keep the full integrity of these forest ecosystems.

References

Angermeier, P.L. and Karr, J.R. 1994. Biological integrity versus biological diversity as policy directions. BioScience, 44: 690-697.

Baskerville, G.L. 1960. Mortality in immature balsam fir following severe budworm defoliation. For. Chron. 36: 342-345.

Baskerville, G.L. 1975. Spruce budworm-super silviculturist. For. Chron. 51: 4-6.

Baskerville, G.L. and MacLean, D.A. 1979. Budworm caused mortality and 20-years recovery in immature balsam fir stands. Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-102.

Batzer, H.O. 1973. Net effect of spruce budworm defoliation on mortality and growth of balsam fir. J. For. 71: 34-37.

Belyea, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. J. For. 50: 729-738.

Bergeron, Y., Leduc, A., Morin, H. and Joyal, C. 1995. Balsam fir mortality following the last
spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. 25: 1375-1384.

Bergeron , Y., Engelmark, O., Harvey, B., Morin, H. and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: introduction. J. Veg. Sci. 9: 464-468.

Bergeron, Y., Harvey, B., Leduc, A. and Gauthier, S. 1999. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. For. Chron. 75(1): 55-61.

Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northern Ontario, with special reference to the physiological age of the tree. For. Chron. 34: 405-422.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. 11: 620-629.

Boivin, J.L. 1977. Régénération après coupes mécanisées et conventionnelles: Côte-Nord du Québec. For. Chron. 53: 341-347.

Bradshaw, F.J. 1992. Quantifying edge effect and patch size for multiple-use silviculture - a discussion paper. For. Ecol. Manage., 48: 249-264.

Burns, R.M. and Honkala, B.H. 1990. Silvics of North America. USDA For. Serv. Agr. Handbook 654. Vol 1, Conifers: 675 p., Vol 2, Harwoods. 877 p.

Carleton, T.J. and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience 1: 141–152.

Cumming, S.G., Schmiegelow, F.K.A. and Burton, P.J. 2000. Gap dynamics in boreal aspen stands : is the forest older than we think? Ecol. Appl. 10: 744-759.

Eis, S. 1967. Establishment and early development of white spruce in the interior British Colombia. For. Chron. 43: 174-177.

Fowells, H.A. 1965. Silvics of forest trees of United States. U.S. Dep. Agric. Handb., n° 271.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems or landscape. Eco. Appl. 3: 202-205.

Frisque, G., Weetman, G.F. and Clemmer, E. 1978. Analyse, 10 après coupe de bois à pâte, des problème de régénération dans l'est du Canada. Forest Engineering Research Institute, Pointe-Claire, Québec, Tech. Rep. TR-23.

Gagnon, R. 1985. Croissance du sapin baumier en relation avec la durée de sa période initiale d'oppression. Master's thesis, Laval University, Québec.

Gauthier, S., Leduc, A. and Bergeron, Y. 1996. Forest dynamics modelling under natural fire cycle: A tool to define natural mosaic diversity in forest management. Environ. Monitoring Asses. 39: 417-434.

Haeussler, S. and Kneeshaw, D.D. 2003. Comparing forest management to natural processes. *In* Towards sustainable management of the boreal forest: emulating nature, minimizing impacts, and supporting communities. *Edited by* P. J. Burton, C. Messier, D. W. Smith and W. L. Adamowicz. NRC Research Press, Ottawa, Ont. pp. 307-368.

Harman, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Ecol. Res., 15: 133-302, USDA Forest Service.

Harvey, B.D. and Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. 19: 1458-1469.

Hatcher, R.J. 1960. Croissance du sapin baumier après une coupe rase dans le Québec. Direction des forêts. Environnement Canada. Mémoire technique no 87.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1-23.

Holling, C.S. and Meffe, G.K. 1996. Command and control and the pathology of natural resource management. Conserv. Biol. 10: 328-337.

Hunter, M.L. 1990. Wild life, forests and forestry :princilples of managing forests for biological diversity. Prentice-Hall Inc., Englewood Cliffs, New Jersey. 370 p.

Jobidon, R. 1995. Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec. Revue de littérature. Mémoire de recherche forestière no 117. Ministère des Ressources naturelles, Québec. 180 p.

Imbeau, L. and Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. J.Wildl. Manage. 66(1): 222-231.

Kneeshaw, D. D., 2001. Are non-fire disturbances important to boreal forest dynamics? Pp 43-58. *Dans* Recent Research Developments in Ecology. *Edited by* S. G. Pandalarai. Transworld Research Press.

Kneeshaw, D.D. and Burton, P.J. 1997. Canopy and age structures of some old sub-boreal Picea stands in British Columbia. J. Veg. Sci. 8: 615-626.

Kneeshaw, D.D. and Bergeron, Y. 1998. Canopy gap caracteristics and tree replacement in the southeastern boreal forest. Ecology, 79(3):783-794.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography and regeneration dynamics of boreal coniferous forest in Finland: a review. Ann. Zool. Fenn. 31: 35-51.

Laflèche, V., Ruel, J.-C. and Archambault, L. 2000. Évaluation de la coupe avec protection de la régénération et des sols comme méthode de régénération de peuplements mélangés du domaine bioclimatique de la sapinière à bouleau jaune de l'est du Québec, Canada. For. Chron. 76(4): 653-663.

Larsson, S. and Danell, K. 2001. Science and management of boreal forest biodiversity. Scand. J. For. Res. 3: 5-9.

Liu and Hytteborn 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J. Veg. Sci. 2: 391-402.

Lieffers, V.J., Messier, C., Burton, P.J., Ruel, J.-C. and Grover, B.E. 2003. Stand level and sylvicultural treatments for sustaining a variety of boreal forest values. *In* Towards sustainable management of the boreal forest: emulating nature, minimizing impacts, and supporting communities. *Edited by* P. J. Burton, C. Messier, D. W. Smith et W. L. Adamowicz. NRC Research Press, Ottawa, Ont. pp. 307-368.

MacLean, D.A., 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56: 213-220.

MacLean, D.A., 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. 60: 273-279.

MacLean, D.A. and Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can. J. For. Res. 19: 1087-1095.

Marchand, S. 1990. Dynamique de la régénération naturelle de jeunes sapinières boréales du centre du Québec. Master's thesis. Laval University. Québec, Québec.

Marquis, D.A. 1965. Scarify soil during logging to increase birch reproduction. North. Log. 14 (5): 24, 42.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. 9: 1-59.

McComb, W. and Lindenmayer, D. 1999.Dying, dead and down trees. *In* Maintaining biodiversity in forest ecosystems. *Edited by* M.L. Hunter, Jr. Cambridge University Press, Cambridge, U.K. pp. 335-372.

McInnis, B.G. and Roberts, M.R. 1994. The effect of full-tree and tree-lenght harvests on natural regeneration. North. J. Applied For. 11: 131-137.

McKenney, D.W., Sims, R.A., Soulé, F.E., Mackey, B.G. and Campbell, K.L. 1994. Towards a set of biodiversity indicators for Canadian Forests. Proceedings of a forest biodiversity indicators workshop. Sault Ste. Marie, Ontario, Nov. 29-Dec.1, 1993, 133 pp.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec. Can. J. For. Res. 24: 730-741.

Morin, H. and Laprise, D. 1989. Histoire récente des épidémies de la Tordeuse des bourgeons de l'épinette au nord du lac Saint-Jean (Québec): une analyse dendrochronologique. Can. J. For. Res. 20: 1-8.

Nealis, V.G. and Régnière, J. 2004. Insect-host relationships influencing disturbance by the spruce budworm in a boreal mixewood forest. Can. J. For. Res. 34: 1870-1882.

Packee, E.C. 1990. White spruce regeneration on a bladed-scarified Alskan Loess soil. North. J. Appl. For. 7: 121-123.

Pastor, J., Light, S. and Sovell, L. 1998. Sustainability and resilience in boreal regions: sources and consequences of variability. Conservation Ecology [online] **2**(2): 16. Available from the Internet. URL:http://www.consecol.org/vol2/iss2/art16/

Perala, D.A. and Alm, A.A. 1990. Reproductive ecology of birch: a review. For. Ecol. Manage. 32: 1-38.

Porter, K.B., Hemens, B. and MacLean D.A. 2004. Using insect-caused patterns of disturbances in northern New Brunswick to inform forest management. *In* Emulating natural forest landscape disturbances. *Edited by* A.H. Perera, L.J. Buse and M.G. Weber. Columbia University Press, New York. pp. 135-145.

Ruel, J.-C. 1992. Impact de la compétition exercée par le framboisier (*Rubus idaus* L.) et les feuillus de lumière sur la croissane du sapin (*Abies Balsamea* (L.) Mill.) en régénération. Can. J. For. Res. 22: 1408-1416.

Ruel, J.-C., Ouellet, F., Plusquellec, R. and Ung, C.-H. 1998. Évolution de la régénération de peuplement résineux et mélangés au cours des 30 années après coupe à blanc mécanisée. For. Chon. 74(3): 428-443.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern Norh America. Ecology, 63: 1533-1546.

Saucier, J.P., Bergeron, J.-F., Grondin, P. and Robitaille, A. 1998. Les régions écologiques du Québec méridional (3[e] version): un des éléments du système hiérarchique de classification écologique du territoire mis au point par le minisère des Ressources Naturelles du Québec, Supplément de L'Aubelle 124: 1-12.

Simard, M.-J., Bergeron, Y. and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. 9: 575-582.

Stiling, P.D. 1996. Ecology: Theories and Practice. Upper Saddle River, NJ: Prentice Hall. Pages 279-280.

Storer, T.I., Usinger, R.L., Stebbins, R.C. and Nybakken, J.W. 1979 General Zoology. New York: McGraw-Hill.

ter Braak, C. J. F. and Smilauer, P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York, USA.

Van Wagner, C.E. 1968: The line intersect method in forest fuel sampling. For. Sci. 14: 20-26.

Warren, W.G. and Olsen, P.F. 1964. A line intercept technique for assessing logging waste. For. Sci. 10: 267–276.

Weetman, G.F. 1965. The need to study silvicultural effects of mechanized logging systems in eastern Canada. For. Chro. 43: 252-256.

Yang, R.C. and Fry, R.D. 1981. Natural succession following harvesting in the boreal mixedwood forest. In: boreal mixedwood symposium. Can. For. Serv. COJFRC symp. Proc. O-P-9. 65-77.

SECTION III: CONCLUSION GÉNÉRALE

Cette étude avait pour but de comparer les effets de la plus récente épidémie de la tordeuse des bourgeons de l'épinette (TBE) en Gaspésie à ceux de la coupe avec protection de la régénération et des sols suivie de l'éclaircie pré-commerciale (CPRS+EPC). L'observation des effets de ces perturbations à deux différentes échelles, soient celle du peuplement et celle du paysage, nous a permis d'évaluer les conséquences écologiques de l'aménagement forestier par rapport à un processus naturel qui semble, à prime abord, avoir des effets semblables sur la forêt. Plusieurs facteurs nous laissent croire que les CPRS+EPC favorisent moins la résilience des peuplements de sapin baumier comparativement à l'épidémie de TBE. Premièrement, sur le plan de la diversité des arbres, la TBE semble favoriser le retour du sapin baumier qui était déjà bien établi sous la canopée avant le passage de l'épidémie, mais également de ses deux principales espèces compagnes, soient l'épinette blanche et le bouleau à papier. Étant moins affectées que le sapin par l'épidémie de TBE, ces espèces laissent plusieurs arbres matures sur les stations sévèrement touchées. L'abondance de chicots et de débris ligneux devraient également favoriser le retour de ces espèces dont la germination des graines est facilitée par le bois en décomposition. À l'opposé, les CPRS+EPC semblent favoriser la dominance du sapin baumier qui pourrait potentiellement conduire à une perte de biodiversité avec la succession des coupes. De plus, les peuplements issus de CPRS+EPC contiennent peu d'éléments structuraux important tels que les arbres résiduels, les chicots et les débris ligneux, et leur variabilité horizontale est inférieure à celle observée suite à l'épidémie de la TBE. Une telle perte d'hétérogénéité et de variabilité pourrait conduire à une diminution de la résilience des forêts aménagées.

À l'échelle du paysage, c'est au niveau de la taille des ouvertures de la canopée que la différence la plus importante a été observée. Pour une même proportion de territoire affecté, les CPRS effectuées entre 1988 et 1998 ont créées des ouvertures environ 200 fois plus grande que celles créées par l'épidémie des années 1970 et 1980. Plus petites, mais plus rapprochées les unes des autres, les ouvertures créées par l'épidémie de la TBE ont formé une fine mosaïque dans le paysage, comparativement à la mosaïque plus grossière engendrée par les CPRS+EPC. Contrairement à nos attentes, la forme des ouvertures créées par la perturbation naturelle était plus régulière que celle des ouvertures créées par l'aménagement forestier. Malgré cela, le ratio périmètre/aire était plus élevé dans les ouvertures créées par l'épidémie étant donné leur taille beaucoup plus petite. Ces ouvertures étaient donc soumises à un effet de bordure plus important.

L'utilisation de deux échelles d'observation dans le cadre d'une même étude nous a permis de faire des liens entre les effets des perturbations observés aux différentes échelles. Par exemple, l'épidémie de TBE a créé une fine mosaïque dans le paysage qui peut constituer, dans une certaine mesure, une forêt irrégulière, puisque la plupart de ces ouvertures sont suffisamment petite pour être entièrement influencée par la forêt qui l'entoure. Ajouté à cela, la structure des peuplements retrouvés dans ces ouvertures présente des caractéristiques de forêt bi-étagée avec certains grands arbres ayant survécu à la perturbation parsemant le jeune peuplement en régénération. Dans ce cas-ci, les effets observés aux deux échelles concordent pour appuyer le caractère plus irrégulier des forêts affectées par une épidémie de la TBE. À l'opposé, les ouvertures créées par les CPRS+EPC sont généralement suffisamment grandes pour constituer des peuplements de structure équienne, et ces peuplements ne contiennent aucun arbre résiduel qui pourrait leur conférer un caractère irrégulier.

Bien que de nombreuses différences aient été mises en évidence par cette comparaison, certains éléments permettent de croire qu'il est possible d'apporter des modifications aux CPRS+ÈPC pour que leurs effets s'approchent davantage de ceux d'une épidémie sévère de la TBE. L'EPC semble jouer un rôle très important dans la succession et la composition des peuplements affectés par les CPRS. Cette intervention semble responsable de la faible proportion de bouleau blanc dans le couvert dominant. Pratiqué judicieusement, l'EPC pourrait permettre de préserver le bouleau blanc, et possiblement l'épinette blanche. La rétention de quelques arbres matures de ces deux espèces sur les parterres de coupe pourrait également favoriser leur persistance dans le domaine bioclimatique de la sapinière à bouleau blanc de la Gaspésie, en plus de favoriser la présence d'éléments structuraux important tels que les chicots et les gros débris ligneux.